

Current Biology

Identifying pterosaur trackmakers provides critical insights into mid-Mesozoic ground invasion

Highlights

- Pterosaur trackmakers are identified using quantitative methods and diagnostic traits
- Three track morphotypes match pterosaur clades inferred as most terrestrially adapted
- Tracks support a mid-Mesozoic radiation of pterosaurs into terrestrial ecosystems
- Identifying trackmakers transforms our view of pterosaur biogeography and ecology

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In brief

Smyth et al. show that pterosaur footprints can be assigned to specific groups using diagnostic traits shared with body fossils. Tracks correspond to clades predicted as the most terrestrially capable, supporting a mid-Mesozoic shift into terrestrial ecosystems. These findings shed new light on pterosaur distribution, habitat use, and ecology.

Article

Identifying pterosaur trackmakers provides critical insights into mid-Mesozoic ground invasion

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<https://doi.org/10.1016/j.cub.2025.04.017>

SUMMARY

Fossilized tracks have provided unique insights into the distribution, behavior, and ecology of extinct taxa. Moreover, because they are abundant and often have distinct distributions in time and space compared with the body fossil record, they have considerable potential for testing and extending macroevolutionary hypotheses. The key to unlocking this vast potential lies in reliably linking tracks to their producers, but this remains a persistent challenge. This limitation is particularly evident among pterosaurs, the dominant flying vertebrates of the Mesozoic. Despite an extensive record of pterosaur tracks spanning more than 100 million years, the identities of trackmakers are unclear in most cases, limiting their use for addressing key questions about pterosaur ecology and evolution. In this study, we employ quantitative analyses and diagnostic features of pedal anatomy to directly link three distinct pterosaur track morphotypes to specific pterodactyloid clades: ctenochasmatooids, dsungaripterids, and neoazhdarchians. These results considerably extend the known biogeographic distribution of these clades, supporting macroevolutionary and ecological hypotheses derived from analyses of the body fossil record. The absence of pterosaur tracks prior to the Middle Jurassic supports evidence from hand and foot morphology indicating that early pterosaurs were arboreal or scansorial. Track evidence demonstrates a major radiation of derived pterodactyloid pterosaurs into terrestrial niches beginning in the Middle Jurassic. Successive clades maintained a strong presence across diverse terrestrial environments throughout the latter half of the Mesozoic, highlighting the evolutionary versatility and ecological significance of pterosaurs in terrestrial environments.

INTRODUCTION

Pterosaurs, flying archosaurian reptiles, were among the most successful tetrapod groups of the Mesozoic (227–66 million years ago [mya]).^{1–3} Historically, their flight capabilities, combined with profound preservation biases,⁴ often led to them being interpreted as aerial specialists closely associated with marine environments.⁵ Pterosaurs were frequently considered ineffectual on the ground, with minimal influence on, or interaction with, terrestrial ecosystems.^{6,7} This traditional perspective suggested that the evolution of flight constrained, rather than expanded, their ecological roles.

However, re-evaluation of pterosaur tracks around the turn of the millennium revealed that at least some species were proficient terrestrial locomotors, employing a quadrupedal gait to navigate on the ground (Figure 1).^{8–13} These discoveries sparked

a renewed wave of research into pterosaur paleobiology, inspiring novel hypotheses about their ecological roles. Reassessments of skeletal morphology,^{3,14–19} flight diversity,²⁰ and dietary adaptations^{21,22} have since demonstrated that pterosaurs occupied a far broader range of ecological niches than previously recognized. Far from being an evolutionary constraint, the development of flight enabled pterosaurs to exploit not only aerial niches but also a wide diversity of terrestrial habitats and ecological roles.¹⁹ This reflects a major shift in our understanding and has profound implications for pterosaur evolutionary history, as well as the nature of their involvement in Mesozoic terrestrial ecosystems.

The pterosaur track record made foundational contributions to modern pterosaur paleontology by settling long-standing debates about terrestrial locomotion that paleontologists had failed to resolve through body fossils alone. Subsequently,

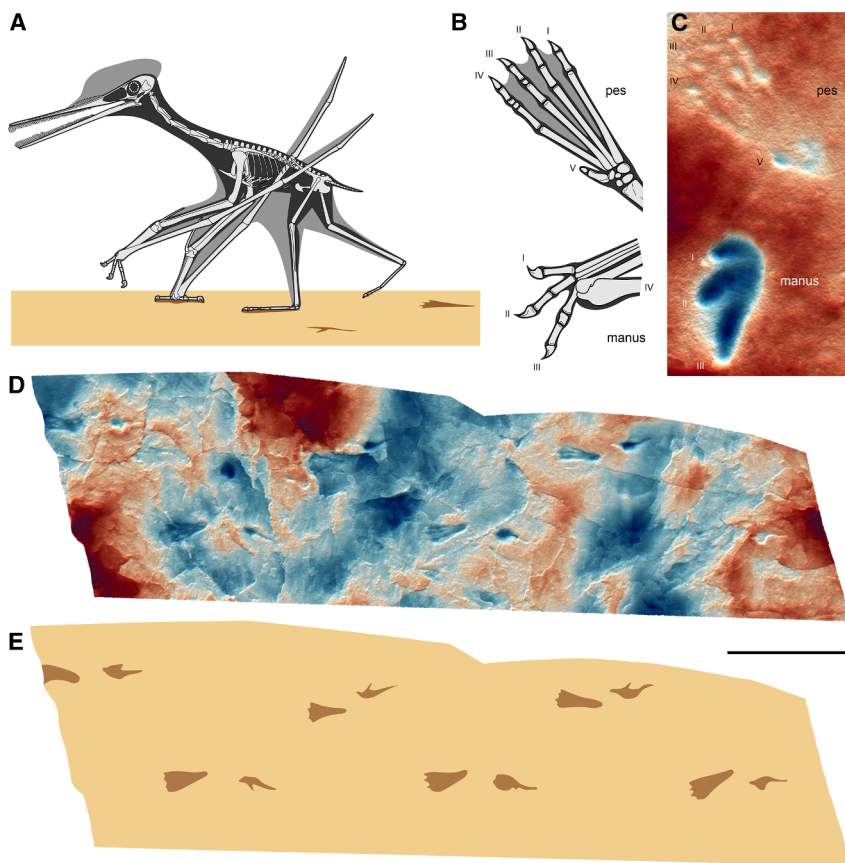


Figure 1. Terrestrial locomotion and track morphology of pterodactyloid pterosaurs

(A) Reconstruction of the ctenochasmatoid pterosaur *Ctenochasma elegans* walking using an ipsilateral gait in which fore and hind limbs on the same side of the body move together as pairs.

(B) Manual and pedal morphology of *Ctenochasma elegans*. The pes is plantigrade and pentadactyl, whereas the manus is digitigrade and functionally tridactyl, as the large fourth digit, which supports the outer wing, is folded away during terrestrial locomotion.

(C) Height map of pterosaur manus and pes footprints in the holotype of the ichnotaxon *Pteraichnus stokesi* (UW 12368), exhibiting a morphology consistent with that of *Ctenochasma elegans*.

(D) Height map of part of a pterosaur trackway, CR99.43 (*Pteraichnus* isp.), from the Upper Jurassic Cazals Formation of Crayssac, France.

(E) Interpretive outline drawing of CR99.43. Range in elevation for (C) and (D) is presented in millimeters. Scale bars: 20 mm in (C) and 200 mm in (D) and (E).

This absence is not without justification. A major obstacle to integrating the body fossil and ichnological records is the difficulty of reliably assigning tracks to specific pterosaur clades. It is generally assumed that all known pterosaur tracks were made by pterodactyloids,^{2,36,37} although this assumption is not universally accepted^{14,25,38} and requires further testing. Attempts to assign tracks to particular clades have typically relied on circumstantial evidence, such as the absolute size of the tracks or their stratigraphic age,³⁹ rather than detailed morphological or quantitative analyses. In rare instances, simple morphological comparisons have been made between tracks and specific body fossil taxa.^{40,41} However, in these cases, the co-occurrence of pterosaur skeletal material and tracks within the same stratigraphic units is often a more convincing justification for assignment than the analyses performed.

Recent advancements in quantitative^{42,43} and synapomorphy-based^{44–46} methods have improved trackmaker assignments for some groups. However, pterosaur trackmaker identification has lagged behind. This is largely due to limited research on the variability of their hands and feet, as well as incomplete adoption of modern three-dimensional (3D) documentation techniques.⁴⁷

In this study, we apply quantitative multivariate analyses and synapomorphy-based methodologies to the global pterosaur track record to identify trackmakers. A newly compiled dataset of pterosaur autopodia enables comprehensive comparisons of skeletal and track records using these approaches. Exceptionally well-preserved tracks can be confidently assigned to specific clades, while even less well-preserved tracks are often attributable to groups based on recognized synapomorphies. The results of this critical reassessment permit testing of the hypothesis that pterosaurs experienced a major ecological shift during the Middle Jurassic.

however, work on pterosaur tracks has become largely disconnected from the main body of pterosaur research. This separation might imply that, having answered the fundamental question about pterosaur terrestrial locomotion, the track record offers little further insight into pterosaur paleobiology. Moreover, most research on pterosaur ecology has predominantly focused on feeding^{21–23} and flight.^{20,24} Although these aspects are crucial, limited knowledge of terrestrial locomotion and habitat use has left a significant gap in our understanding of broader pterosaur ecology.

Over the past 30 years, many new occurrences of pterosaur tracks have been discovered, to the point that tracks potentially rival body fossils in terms of material abundance.^{25,26} This rich record represents a unique and underutilized source of data for pterosaur paleobiology. Unlike body fossils, which can be moved from their original location, tracks usually remain in the same place where they were formed.

As a result, tracks offer unparalleled information about the behavior, movement, and interactions of extinct animals as living animals in their natural habitats, capturing aspects of their lives that body fossils alone cannot reveal.^{27–31} Pterosaur tracks also remain neglected in broader paleontological studies. Tracks are often preserved in depositional environments that differ distinctly—stratigraphically, geographically, and ecologically—from those yielding body fossils. However, these data have not yet been successfully incorporated into studies of pterosaur distribution,³² ecology,³³ and macroevolution.^{34,35}

RESULTS

This analysis prioritizes pes prints over manus prints, as manus morphology is more conservative across Pterosauria, and the lack of clear osteological correlates limits comparisons with skeletal remains (see [STAR Methods](#) for details). Nevertheless, the elongated digit III of most pterosaur manus prints indicates that the trackmakers had strongly ectaxonic manual digits. Although this characteristic offers limited specificity for identifying individual trackmakers, it does suggest that clades with more equally proportioned manual digits, such as anurognathids, scaphognathines, istiodactylids, and ornithocheirids,¹⁹ are not likely to have produced any of the pterosaur tracks reported to date.

Pes prints provide a more practical basis for identifying trackmakers. Exceptionally well-preserved pterosaur specimens with intact soft tissue demonstrate that their feet had relatively minimal soft tissue, with comparatively small footpads when contrasted with most other Mesozoic archosaurs.^{48–50} This observation aligns with expectations, as mechanical and aerodynamic selective pressures favor the concentration of muscular mass in the proximal portion of the limb, a pattern also seen in extant flying vertebrates.^{51,52}

Pterosaur footpads had a predominantly arthral arrangement, with each pad placed at the position of a metatarsophalangeal (MTP) or interphalangeal (IP) joint ([Figures 2A and 2B](#)).^{8,48,53} The only exceptions are in the proximal IP pads of digits III–IV of monofenestrated pterosaurs, where the intermediate phalanges of pedal digits III (PPh III-2) and digit IV (PPh IV-2, IV-3) are greatly reduced to tiny menisci of bone.⁵³ This arrangement divides the digits into two functional mechanical units: a proximal and a distal section, separated by a single footpad that encloses the distal end of the proximal phalanx, the greatly reduced intermediate phalanx or phalanges, and the proximal end of the penultimate phalanx ([Figures 2A and 2B](#)).

Small, discrete digital footpads, preserved in “elite” pterosaur pes prints (i.e., those recording high anatomical fidelity),⁵⁴ correspond to 11 joint locations, which serve as anatomical landmarks reflecting the underlying skeletal structure of the trackmaker ([Figure 2C](#)). These landmarks allow for direct comparisons between the pedal morphology of trackmakers and pterosaur foot skeletons from the body fossil record ([Figures 1B, 1C, and 2A–2C](#)), using both quantitative analyses and synapomorphy-based approaches. By utilizing these methodologies, it is possible to discriminate between pterosaur and non-pterosaur tracks and among pterosaur clades. All reported pterosaur prints preserving sufficient anatomical information can be assigned to pterodactyloid trackmakers, with no known examples of non-pterodactyloid trackmakers. Furthermore, we have identified three distinct pes print morphologies, each corresponding to a recognized pterodactyloid clade ([Figure 2D](#)).

Pterodactyloid morphotype 1: Ctenochasmatoïd trackmakers

The most abundant pterosaur track type, based on documented prints, is characterized by large, subtriangular pes prints relative to their smaller manus prints ([Figures 1C, 3A–3C, and 3E–3H](#)). The pes prints possess elongate metatarsals with relatively short digits. These tracks were the first to be identified and were central to debates from the 1980s to early 2000s regarding whether

Pteraichnus trackmakers were crocodylomorphs^{53,55} or pterosaurs.^{8–10,12,13} This is the only pterosaur track morphotype recorded in the Jurassic and remains the most common form in the lowermost Cretaceous. It is represented by many ichnospecies within *Pteraichnus*, including *Pt. saltwashensis*,⁵⁶ *Pt. stokesi*,⁸ *Pt. palacieisaenzi*,^{57,58} *Pt. longipodus*,⁵⁹ “*Pt. vetustior*,”⁶⁰ and many more tracks referred to *Pteraichnus* isp, as well as *Purbeckopus pentadactylus*^{51,62} ([supplemental information](#)).

The pes prints are distinguished from those of other pterosaurs by an unusual metatarsal formula, indicated by the positions of the MTP joints. In these prints, metatarsal I is notably longer than the rest, which decrease in length laterally, resulting in the metatarsal formula I > II > III > IV ([Figure 3C](#)). This arrangement is highly atypical for diapsids, making tracks of this morphotype easily distinguishable from many other potential trackmakers. Importantly, it excludes crocodylomorphs as potential trackmakers due to their relatively short metatarsal I.⁵⁰

Among reptiles, this metatarsal formula occurs only in certain pterosaurs, including *Ardeadactylus longicollum*, *Aurorazhdarcho micronyx*, *Balaenognathus maeuseri* ([Figures 2B and 3D](#)), and *Ctenochasma elegans* ([Figure 1B](#)) from the Upper Jurassic (Kimmeridgian-Tithonian) of southern Germany,^{63–65} *Pterodaustro guinazui* from the Lower Cretaceous (Albian) of central Argentina,⁶⁶ and *Sinopterus dongi* from the Lower Cretaceous (Barremian-Aptian) of northeast China.⁶⁷ Although *Sinopterus dongi* shares this metatarsal formula, other morphological traits, including a proportionately shorter metatarsus, short proximal digits, and elongate distal digits, definitively exclude tapejarids as potential trackmakers. By contrast, the remaining species all belong to European and South American members of the clade Ctenochasmatoïdea. Additional anatomical features confirm that ctenochasmatoïds produced tracks of this morphotype.

The metatarsal region in these prints is consistently elongated, often more than twice the length of the digital region ([Figures 3A–3C and 3E–3H](#)), aligning with the highly elongated metatarsals seen in ctenochasmatoïds ([Figure 3D](#)). The subtriangular shape of the pes prints and the frequent impressions of the metatarsal shafts demonstrate that the metatarsals were splayed in life. This splayed arrangement is found only in two groups of pterodactyloids: euctenochasmatoïans (which include *Pterodactylus* and ctenochasmatoïds) and ornithocheiroïds (istiodactylids, ornithocheiroïds, and pteranodontians). However, the elongation of the metatarsals and their relative proportions rule out ornithocheiroïds as potential trackmakers. Similarly, the proportions of the digits, characterized by relatively elongated proximal segments and shortened distal segments, are consistent with those of ctenochasmatoïds ([Figure 3D](#)). Furthermore, the splayed feet of euctenochasmatoïans are known to have supported intermetatarsal and interdigital webbing.⁴⁸ Consistent with this, evidence of webbing can be observed in many of these prints ([Figures 3A–3C, 3F, and 3H](#)).

In a few cases, these tracks preserve a small impression of the much-reduced digit V ([Figures 1C and 3A–3C](#)). This has sometimes been interpreted as evidence of potential non-pterodactyloid trackmakers,²⁵ which are known to have possessed a well-developed pedal digit V. However, this feature alone is insufficient to support a non-pterodactyloid affinity, and the proportions of the other pedal elements mentioned above are inconsistent with any non-pterodactyloid pterosaur. Most

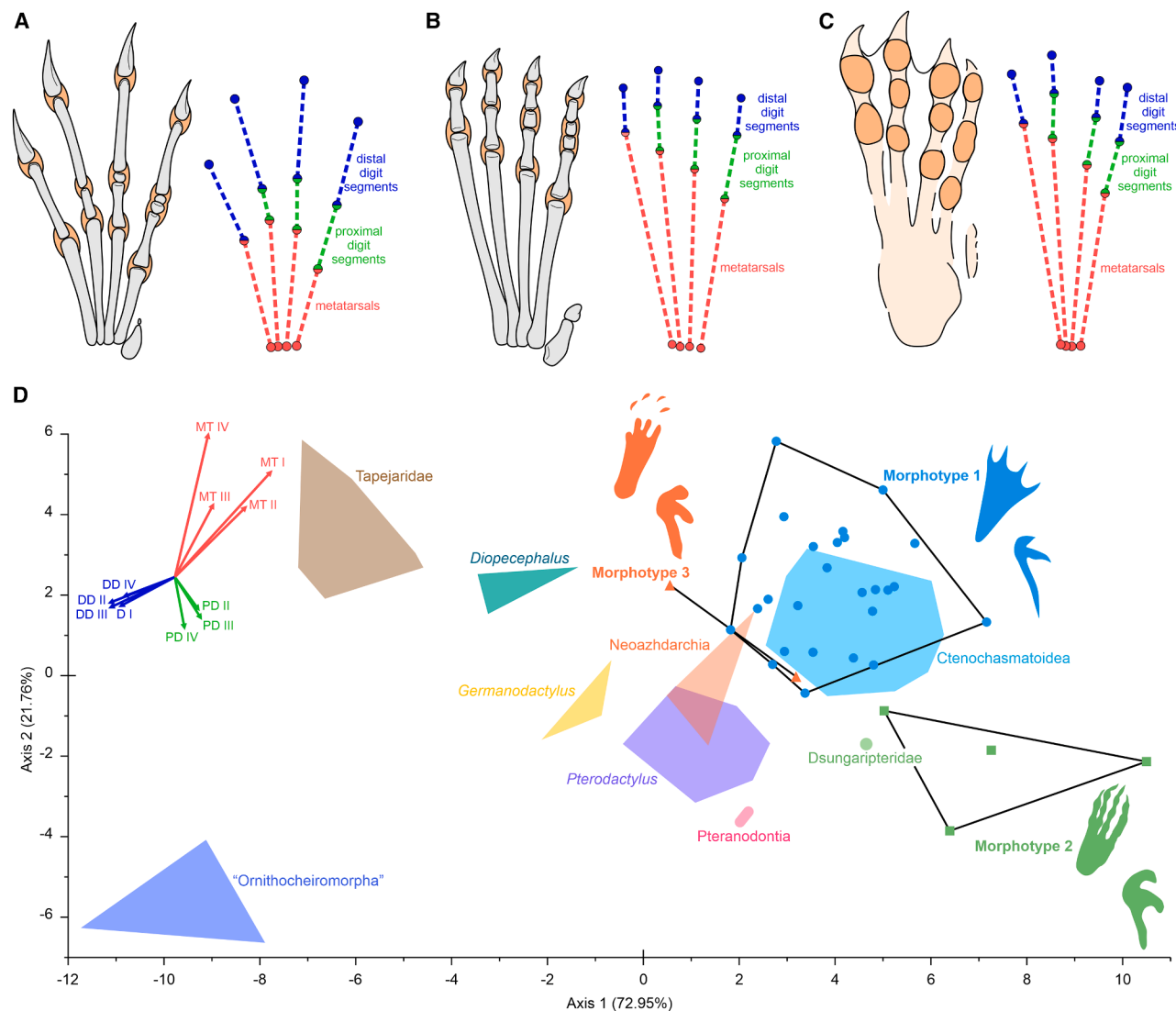


Figure 2. Disparity in pterodactyloid pedal morphology

(A) Foot of an indeterminate “ornithocheiromorph” (SDUST-V1006) with positions of arthral footpads indicated and a schematic representation showing the anatomical regions used in this analysis. Typical of “ornithocheiromorphs”, it exhibits short metatarsals and elongated distal digits.

(B) Foot of the ctenochasmatoid *Balaenognathus maeuseri* (NKMB P2011-633) with positions of arthral footpads indicated and a schematic representation separated into its anatomical regions. In contrast to the feet of “ornithocheiromorphs”, those of ctenochasmatoids exhibit greatly elongated metatarsals and shortened distal digits.

(C) Illustrative drawing of a pterosaur pes print, *Pterainchus* isp. (UW 39958), with arthral joint positions highlighted and schematic representation showing the anatomical regions. The proportions of this print match closely with those of ctenochasmatoids.

(D) Biplot of the first two axes of linear discriminant analysis, illustrating variation in the pedal proportions among the principal pterodactyloid clades and the three pterodactyloid track morphotypes. Shaded hulls represent morphospace occupied by pedal anatomy of pterodactyloid body fossil groups. Black hull outlines represent extent of pterosaur track morphotypes. Blue circles, track morphotype 1; green squares, track morphotype 2; orange triangles, track morphotype 3. Metatarsal length is positively associated with both axis 1 and axis 2. Proximal digit length is positively associated with axis 1 and negatively associated with axis 2. Distal digit length shows a negative association with both axis 1 and axis 2. Relative arrow lengths represent the contribution of each region to the class separation in the reduced-dimensional space.

Abbreviations: DD, distal digit segment; MT, metatarsal; PD, proximal digit segment.

See [Figures S1–S4](#) and [Data S1](#) for more details.

pterodactyloids retain a much-reduced digit V ([Figures 1B, 2A, and 2C](#)), and in ctenochasmatoids, it can remain prominent ([Figure 3D](#)). The combined length of metatarsal V and digit V accounts for 15%–20% of the total foot length, consistent with observed proportions of these tracks.

Elite tracks with this morphology were photogrammetrically documented from four major Upper Jurassic geological units. This included the Summerville and Sundance formations (Oxfordian) of the western USA ([Figures 1C, 3B, 3E, and 3F](#)); the Lastres Formation (Kimmeridgian-Tithonian) of Asturias, northwest Spain

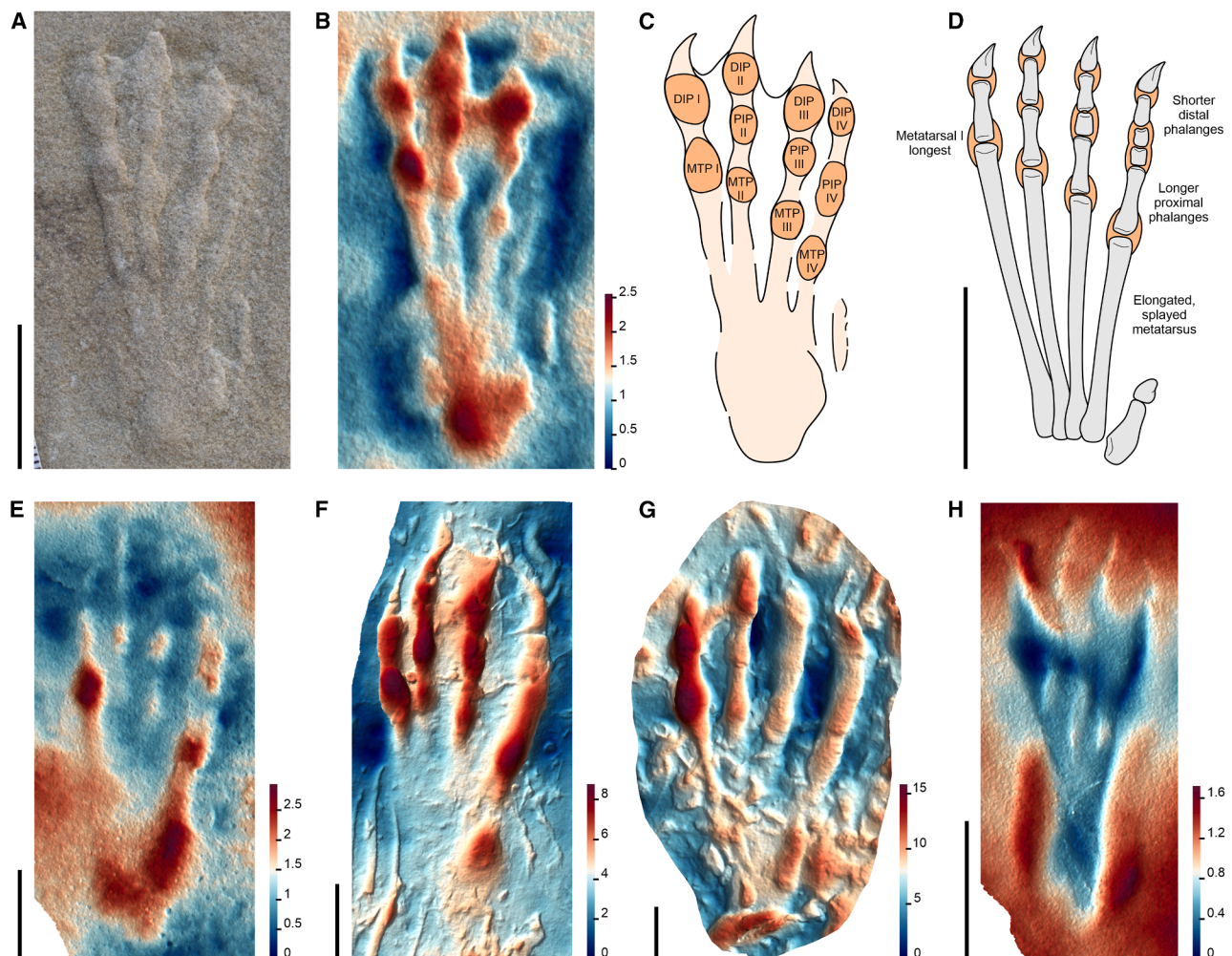


Figure 3. Pterosaur track morphotype 1: Ctenochasmatoid trackmakers

(A) Photograph of the natural cast of the pes print of *Pteraiichnus* isp. (UW 39958) from Seminoe reservoir, Wyoming, USA, Upper Jurassic Sundance Formation. (B) Height map of *Pteraiichnus* isp. (UW 39958) showing the position of arthral footpads. (C) Interpretative line drawing of *Pteraiichnus* isp. (UW 39958), with individual footpads labeled. (D) Pedal anatomy of the ctenochasmatoid *Balaenognathus maeuseri* (NKMB P2011-633) with features shared with tracks of morphotype 1 labeled. (E) Height map of *Pteraiichnus* isp. (UW 33641), an artificial cast, from Alcova Reservoir, Wyoming, USA, Upper Jurassic Sundance Formation. (F) Height map of *Pteraiichnus* isp. (UCM 188.46), a natural cast, from Del Monte Mines, Utah, USA, Upper Jurassic Summerville Formation. (G) Height map of *Pteraiichnus* isp. (UCM 198.12), an artificial cast, from Asturias, Spain, Upper Jurassic Lastres Formation. (H) Height map of *Pteraiichnus* isp. (CR98.33), a natural impression, from Crayssac, France, Upper Jurassic Cazals Formation. (E), (F), and (H) Are mirrored for comparative consistency. Abbreviations: DIP, distal interphalangeal footpad; PIP, proximal interphalangeal footpad; MTP, metatarsophalangeal footpad.

Range in elevation for height maps presented in millimeters. Scale bars, 20 mm.

See [Data S1](#) for more details.

(Figure 3G); and the Cazals Formation (Tithonian) of Crayssac, southwest France (Figures 1D and 3H). Linear discriminant analysis (LDA) (Figure 2D) classified 96% of morphotype 1 tracks as ctenochasmatoid, with one print (UCM 187.21 P-45a) being recovered as *Pterodactylus*, the sister taxon to Ctenochasmatoidea.

Although only a small fraction of prints can be classified as elite and preserve all the footpad impressions necessary for quantitative analysis, many more prints retain enough diagnostic features, such as a splayed pes with elongate metatarsals exhibiting the formula $I > II > III > IV$, sufficient to assign them to ctenochasmatoid trackmakers.

Pterodactyloid morphotype 2: Dsungaripterid trackmakers

Recorded only from the Lower Cretaceous (Berriasian-Valanginian) Tugulu Group of the Junggar Basin in northern Xinjiang, China, this is the rarest and most spatiotemporally restricted track morphotype (Figure 4). Ichnotaxa belonging to this morphotype include *Pt. wuerhoensis*⁴⁰ (Figure 4A–4C) and *Pt. junggarensis*.^{41,68}

These prints differ from those of ctenochasmatoids in several respects. Unlike ctenochasmatoids, where metatarsal I is the longest, here it is slightly shorter than or subequal in length to

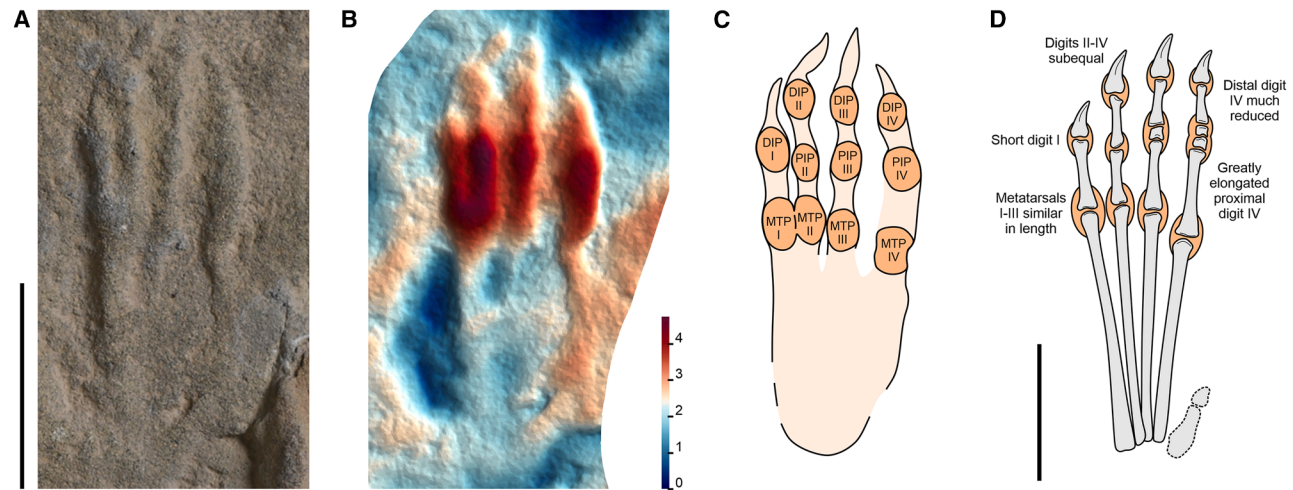


Figure 4. Pterosaur track morphotype 2: Dsungaripterid trackmakers

(A) Photograph of the natural cast of the pes print of *Pterainchus wuerhoensis* (IVPP V 26281.2 58PR) from Huangyangquan Reservoir tracksite 1, Xinjiang, China, Lower Cretaceous, Shengjinkou Formation. Reproduced from Li et al.⁴⁰

(B) Height map of *Pterainchus wuerhoensis* (IVPP V 26281.2 58PR) showing the position of arthral footpads.

(C) Interpretative line drawing of *Pterainchus wuerhoensis* (IVPP V 26281.2 58PR), with individual footpads labeled.

(D) Pedal anatomy of the dsungaripterid *Noripterus complicitens* (IVPP RV 73001), with features shared with tracks of morphotype 2 labeled.

(A)–(C) Are mirrored for comparative consistency. Abbreviations: DIP, distal interphalangeal footpad; MTP, metatarsophalangeal footpad; PIP, proximal interphalangeal footpad.

Range in elevation for height maps presented in millimeters. Scale bars, 20 mm.

See [Data S1](#) for more details.

metatarsal II (Figures 4A–4C), representing the plesiomorphic condition for pterosaurs. Additionally, the entire metatarsus is proportionally shorter than in ctenochasmatooid prints.

The proximal segments of digits II–IV are elongated, while digit I and the distal segments of digits II–IV are significantly reduced. As a result, digit I does not extend as far distally, often terminating well before digits II–IV, creating a pattern of a shorter digit I and longer, subequal digits II–IV (Figures 4A–4C). This differs from most pterosaurs, where all four digits extend anteriorly to a similar distance, with digits II–III extending slightly further and remaining subequal in length.

These digital proportions occur in the dsungaripterids *Dsungaripterus weii* and *Noripterus complicitens* (Figure 4D) as well as the pteranodontian *Pteranodon*. However, the proportionately shorter metatarsals, somewhat longer penultimate phalanges, and extensive splaying of the metatarsals exhibited by *Pteranodon* are inconsistent with tracks of this morphotype.

Reduction of penultimate phalanx length is most apparent in the morphology of digit IV of both dsungaripterid feet and tracks of morphotype 2 (Figures 4A–4D). Elongation of PPh IV-1 contrasts with a significantly reduced PPh IV-4, less than half of the length of PPh IV-1. This diagnostic morphology distinguishes the pes of dsungaripterids from other pterosaurs.

Four pes prints on the holotype slab of *Pt. wuerhoensis* (IVPP V 26281.2) were suitable for quantitative analysis (Figure 2D). LDA classified all four elite prints to a dsungaripterid trackmaker. However, these results should be interpreted with caution due to the limited skeletal sample sizes as only one example of a complete dsungaripterid pes is currently known.

It has been suggested that tracks of this morphotype can be attributed to specific body fossil species. For example, *Pt.*

wuerhoensis has been proposed to have been produced by *Noripterus complicitens*, whereas *Pt. junggarensis* prints were attributed to *Dsungaripterus weii*, based on similarities in size, digit-to-metatarsal ratios, and a notably shorter digit I impression compared with digits II–IV.^{40,41} We find it difficult to justify assigning these tracks to species-level taxa. Only a single complete dsungaripterid foot is known, and the short first digit used to attribute these prints to *Noripterus* is also present in *Dsungaripterus* (IVPP V 28299). Moreover, comparable digit-to-metatarsal ratios are found across different pterodactyloid clades, making this an unreliable criterion for species-level identification. Size alone is also not a justification for a species-level assignment, as smaller tracks could easily represent immature individuals of a larger taxon.

Pterodactyloid morphotype 3: Neoazhdarchian trackmakers

This morphotype is geographically widespread, with reports from Africa, Asia, and North America. It is characterized by narrow, elongated pes prints with faint digital impressions (Figures 5A and 5B). Unlike other morphologies, a deeply impressed, subcircular heel-print is typically the most prominent feature. Due to the less pronounced impression of the distal digital region, preservation is often limited to the proximal portions of the digits. Prominent claw marks may be present, although they are often separate from the rest of the impression. These unusual features clearly distinguish these prints from those of both ctenochasmatooids and dsungaripterids.

Although prints of this morphotype exhibiting high anatomical fidelity are scarce, diagnostic features permit confident identification of azhdarchoid trackmakers (Figures 5C–5E). Unlike

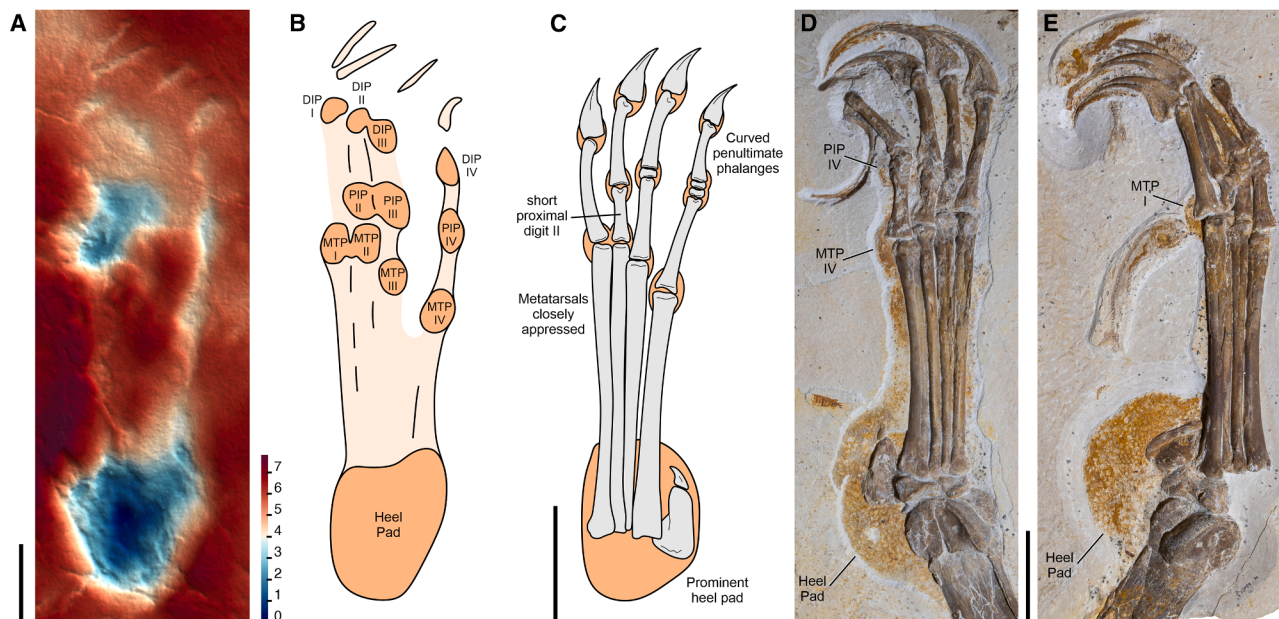


Figure 5. Pterosaur track morphotype 3: Neoazhdarchian trackmakers

(A) Height map of a natural cast of *Pteraichnus yanguoxiaensis* (UCM 214.53) showing the position of arthral footpads and large heel pad.

(B) Interpretative line drawing of *Pteraichnus yanguoxiaensis* (UCM 214.53), with individual footpads labeled.

(C) Pedal anatomy of the chaoyangopterid neoazhdarchian *Meilifeilong sanyainus* (DB0233), with features shared with tracks of morphotype 3 labeled.

(D and E) Left and right feet of an indeterminate tapejarid azhdarchoid (SMNK PAL 3830). Exceptional preservation of soft tissue shows the presence of both arthral footpads and prominent heel pads.

Abbreviations: DIP, distal interphalangeal footpad; MTP, metatarsophalangeal footpad; PIP, proximal interphalangeal footpad.

Range in elevation for height maps presented in millimeters. Scale bars, 20 mm.

See [Data S1](#) for more details.

most pterodactyls, which have relatively shallow heel pads comparable to other pedal pads,⁴⁸ azhdarchoids exhibit well-developed, stout, hemispherical heel pads. Although autopodial soft tissues of most azhdarchoid clades are unknown, they have been documented in an exceptionally preserved tapejarid (Figures 5D and 5E).⁴⁸ These soft tissue structures are likely synapomorphic for all azhdarchoids (Figure 5C).¹⁵

Although approximate metatarsal lengths can rarely be ascertained, MTP joint impressions show that metatarsal I is subequal in length or shorter than metatarsal II, distinguishing these tracks from those of ctenochasmatooids (Figures 5A and 5B). The elongated and narrow impression of the metatarsus indicates that the metatarsals were tightly appressed. Among pterodactyls, only *Diopecephalus*, “germanodactylids”, dsungaripterids, and azhdarchoids are known to have possessed closely appressed metatarsals.^{15,69,70}

The autopodia of non-tapejarid azhdarchoids remain relatively poorly understood, with limited information available for neoazhdarchians such as thalassodromeids, chaoyangopterids, and azhdarchids. However, many tracks exhibiting this morphotype can be confidently attributed to neoazhdarchians based on distinct preserved features, as even partial evidence—such as a few MTP or interdigital pads—can permit the identification of these pterosaurs.

For example, in this morphotype, the proximal segment of digit III is slightly longer than its distal segment, whereas in digit IV, the proximal segment is significantly longer than the distal segment

(Figures 5A and 5B). This contrasts sharply with the pedal morphology of all known tapejarids, where the proximal segment of digit III is much shorter than its respective distal segment, and the proximal and distal segments of digit IV are approximately equal in length (Figures 5D and 5E).¹⁹ The morphology observed in these prints aligns with the pedal proportions of all known neoazhdarchians, including the thalassodromeid *Tupuxuara leonardii* (D.M.U., data not shown), the azhdarchid *Zhejiangopterus linhaiensis*,⁷¹ and chaoyangopterids such as *Jidapterus edentus*,⁷² *Meilifeilong sanyainus* (Figure 5C),⁷³ *Meilifeilong youhao*,⁷⁴ *Shenzhoupterus chaoyangensis*,⁷⁵ and an undescribed specimen (LPM-L112113).⁷²

Despite this morphotype’s wide distribution, the typical morphology of the track types discussed above means that exceptionally preserved prints with detailed footpad structures are very rare, limiting the data available for quantitative comparison. Only two specimens, *Agadirichnus elegans* (FSA.G.54)⁷¹ and *Pteraichnus yanguoxiaensis* (UCM 214.53),⁷⁶ preserved all the necessary landmarks. LDA classified both prints as neoazhdarchian based on similarities in pedal proportions with azhdarchids (*Zhejiangopterus linhaiensis*) and chaoyangopterids (*Jidapterus edentus* and *Meilifeilong sanyainus*) (Figure 2D). However, the rarity of elite prints, combined with morphospace overlap between *Agadirichnus elegans* and morphotype 1 (identified as being produced by ctenochasmatooids), makes determination of quantitative distinctness difficult. Furthermore, the large hemispherical heel pad impression of neoazhdarchian

prints certainly produces a greater overestimation of metatarsus length relative to other groups, further complicating the distinction between morphotypes. As such, a referral to trackmakers based on synapomorphies rather than quantitative analysis is more effective for identifying most morphotype 3 tracks.

DISCUSSION

Limitations of current ichnotaxonomy

A full reassessment of pterosaur ichnotaxonomy is beyond this study's scope and will be discussed elsewhere, but key limitations merit discussion. Current practices overlook distinctive morphological features, relying instead on simple metrics like manus/pes ratios, digit angles, or size. These parameters are likely only weakly correlated with print morphology or trackmaker anatomy. For instance, tracks assigned to *Pteraichnus* span all three morphotypes, despite major distinctions, whereas ichnotaxa like *Haenamichnus uhangriensis*³⁹ seem defined by size or preservation rather than true morphology. A refined approach, prioritizing morphology over basic dimensions or sedimentological factors, would enhance their interpretive value.

Spatiotemporal distribution of pterosaur tracks

The methodology employed here enhances the utility of the track record by allowing direct comparison of the temporal distribution of track morphotypes with the body fossil record of their respective track-making clades. Reports of putative pterosaur tracks from various global sites were re-evaluated, with verified tracks classified into morphotypes 1, 2, or 3 (Figure 6) or as indeterminate pterodactyls if they lacked preserved pes impressions or sufficient morphological detail (Figure S5).

No tracks were identified as being produced by non-pterodactyls, despite the presence of several diagnostic features in non-pterodactyl autopodia that would be evident in their tracks. These include manus impressions with more equally sized digits and larger claw impressions than those found in any known pterodactyl tracks, proportionally larger intermediate phalanges in pedal digits III–IV, elongated penultimate pedal phalanges in all but the most basal forms, and likely an elongate pedal digit V comparable in length to the other digits. None of these characteristics were observed among pterosaur tracks. Other tracks initially identified as pterosaurian but reclassified as ambiguous or incorrectly attributed were excluded from the dataset (see STAR Methods).

Despite the fragmentary nature of the pterosaur body fossil record, a strong congruence is observed between the distribution of pterosaur tracks attributed to specific clades and the temporal occurrence of their corresponding body fossils (Figure 6). This temporal coincidence strengthens the interpretations of trackmaker identity and clade-specific evolutionary patterns.

All confirmed pterosaur tracks date from the Middle Jurassic to the end-Cretaceous, aligning closely with the pterodactyl body fossil record (Figure 6), with the only discordance being the slightly earlier appearance of pterodactyl tracks. Track morphotypes linked to ctenochasmoids, dsungaripterids, and neoazhdarchians also show strong congruence with body fossils.

The oldest definitive pterodactyl skeletal remains are those of the ctenochasmoid *Liaodactylus primus*, from the

Oxfordian-aged Tiaojishan Formation of Liaoning, China.³³ However, based on current phylogenetic hypotheses, ctenochasmoids are inferred to have been present as early as the Middle Jurassic.^{19,77} Body fossil evidence indicates that ctenochasmoids were the most diverse group of pterodactyls during the Upper Jurassic and remained a significant component of pterosaur diversity into the earliest Cretaceous.⁷⁸ Their diversity declined in the latter half of the Lower Cretaceous, and they appear to have gone extinct by the beginning of the Upper Cretaceous.⁷⁸

This temporal distribution corresponds closely to the early history of the pterosaur track record. The first definitive ctenochasmoid tracks also occur in the Oxfordian, but some of uncertain age may extend as far back as the Bathonian (Figure 6). Earlier purported pterosaur tracks are less than convincing and show no definitive diagnostic characters of pterosaur tracks (see STAR Methods).

Ctenochasmoid tracks, the only pterosaur tracks known from the Jurassic, remain the most common form in the early Lower Cretaceous, predominantly found in shallow marine carbonate deposits from the Upper Jurassic and earliest Cretaceous (Berriasian), associated with the epicontinental Sundance Sea in North America and the European Archipelago (Figure 6).²⁵ In contrast to the body fossil record, there are currently no confirmed ctenochasmoid tracks documented after the Berriasian. The absence of ctenochasmoid tracks in the remainder of the Lower Cretaceous, despite the continued presence of skeletal remains from this clade, likely stems from a significant decline in the number of known pterosaur tracksites during this interval. This decline is particularly notable in the near absence of shallow marine carbonate tracksites in which ctenochasmoid tracks are abundant during earlier periods. This reduction in marginal marine carbonate tracksites is indicative of a broader sampling bias that is not unique to the pterosaur fossil record but is also evident in other Mesozoic tetrapod groups such as dinosaurs.⁷⁹

Little is known about the paleobiogeographic distribution of dsungaripterids. The earliest potential dsungaripterid material consists of fragmentary remains from the Upper Jurassic (Kimmeridgian) of Europe.⁸⁰ An Upper Jurassic origin appears likely, as by the earliest Cretaceous (Berriasian–Valanginian), dsungaripterids had likely already achieved a broad distribution, with a relatively good record in Asia,⁸¹ fragmentary remains from South America,⁸² and possible occurrences in Europe.⁸³ Most dsungaripterid fossils are found in Lower Cretaceous strata in northeast Asia, including Xinjiang in northwest China, particularly the Junggar Basin,⁸⁴ as well as Mongolia,⁸⁵ possibly Japan,⁸⁶ and Siberia.⁸⁷ Three named dsungaripterid taxa are currently recognized from the Tugulu Group of the Junggar Basin: *Dsungaripterus weii*, *Lonchognathosaurus acutirostris*, and *Noriopteris complicidens*. There is currently no definitive evidence that dsungaripterids persisted beyond the Early Cretaceous, with evidence for their post-Valanginian survival hinging on the uncertain minimum depositional age of the Lianmuqin Formation.⁸⁴

Like their patchy body fossil record, dsungaripterid tracks are the rarest and most spatiotemporally restricted track morphotype identified in this study. Tracks of this type have so far only been recorded in the Valanginian Shengjinkou Formation in the Tugulu Group of the Junggar Basin in northern Xinjiang, China

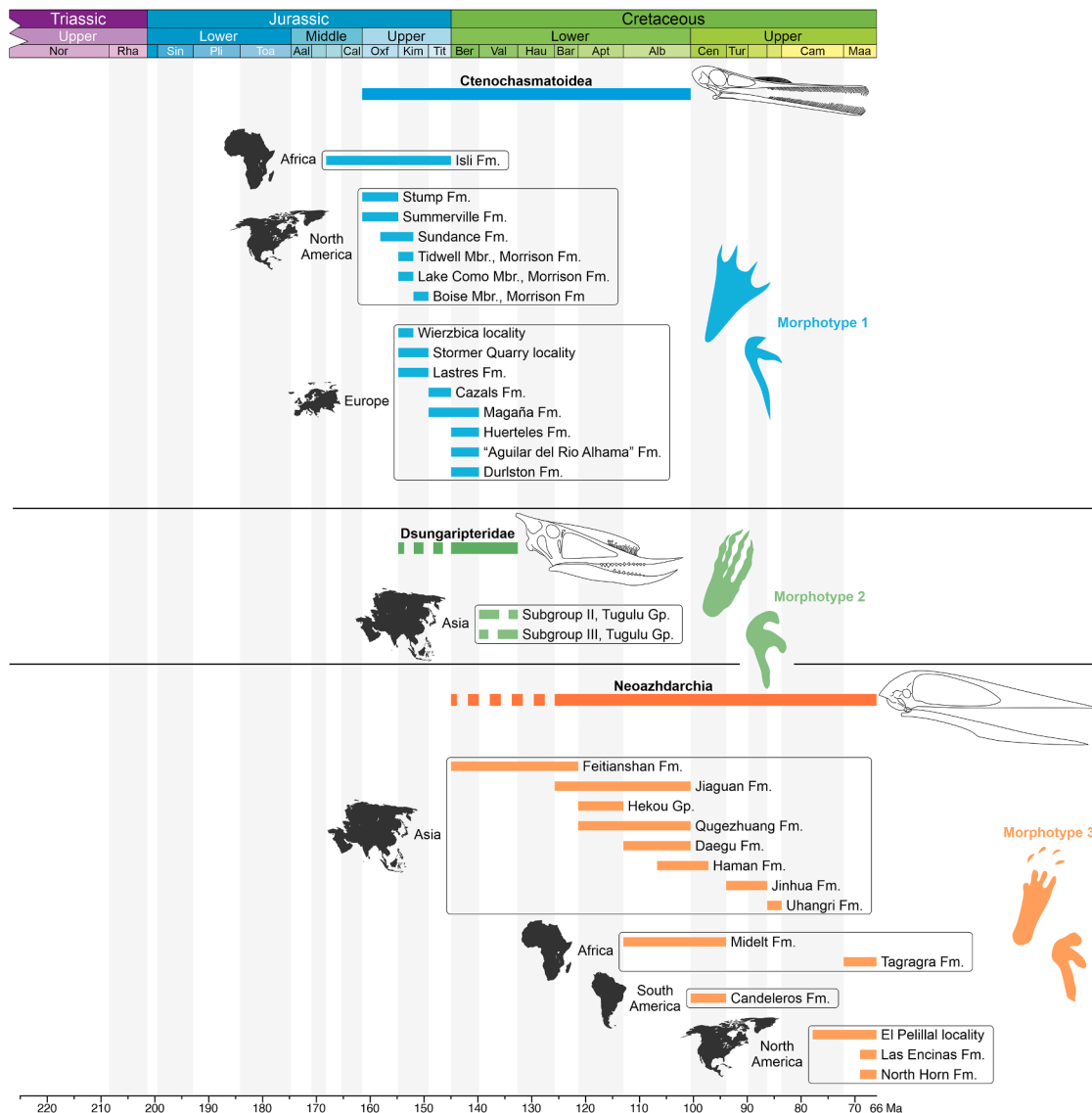


Figure 6. Temporal distribution of body fossils and tracks for the three track-making clades

The temporal ranges of body fossil records, represented by skulls, closely correspond to the temporal distribution of tracks. Refer to Figure S5 for the distribution of indeterminate pterodactyloid tracks.

See Data S1 for more details.

(Figure 6).^{40,41,68,84,88} The Shengjinkou Formation is unique in the pterosaur record as it is currently the only sequence in the world that produces abundant pterosaur track layers intercalated with beds that yield significant pterosaur skeletal remains. Tracks matching dsungaripterid pedal morphology occur in gray sandstone units,⁴⁰ while a near-exclusive dsungaripterid pterosaur skeletal record comprising *Dsungaripterus weii* and *Noripterus complicidens* has been recovered from gray-green mudstone facies within the Shengjinkou Formation.⁸⁴ This unique co-occurrence provides an opportunity to test the validity of the trackmaker hypothesis with a high degree of confidence, as both skeletal remains and tracks indicate dsungaripterid-dominated assemblages.

The earliest putative azhdarchoid skeletal material occurs in the lowermost Cretaceous of Romania.⁸³ The first definitive evidence of azhdarchoids comes from tapejarids in the early Barremian Yixian Formation of Liaoning, China.⁶⁷ Neoazhdarchians appear slightly later, in the latest Barremian-early Aptian Jiufotang Formation, also in Liaoning⁸⁹ (Figure 6). However, their body fossil record soon becomes widespread, and by the close of the Lower Cretaceous, neoazhdarchians had likely achieved a global distribution, with significant fossils from South America,⁹⁰ Africa,^{90,91} and fragmentary remains in North America.⁹²

Azhdarchids are the only clade of neoazhdarchians known to have survived a major faunal turnover at the Cenomanian-Turonian boundary, continuing into the latest Cretaceous.²

Body fossils from this period have been discovered on every continent except Antarctica.⁹³ As well as attaining a global distribution, azhdarchids were a diverse and long-lived clade, thriving up until the K-Pg extinction event, which marked the disappearance of all pterosaurs at the end of the Cretaceous.^{77,93}

Neozhdarchian tracks represent the only pterosaur tracks identified from the late Lower Cretaceous (post-Valanginian) through to the end of the Cretaceous, with their distribution closely mirroring those of the body fossil record (Figure 6). These tracks first appear in the early Lower Cretaceous of China, approximately contemporaneous with the earliest definitive skeletal remains of the group. However, the imprecise dating of stratigraphic units such as the Feitianshan⁹⁴ and Jiaguan⁹⁵ formations obscures the precise timing of their initial occurrence. During the late Lower Cretaceous, neozhdarchian tracks persist in China and appear in Korea. By the mid-Cretaceous (Albian-Cenomanian), they are documented in North Africa, coinciding with abundant neozhdarchian fossils from the Kem Kem Group,^{91,96} as well as in South America.

The Upper Cretaceous record includes *Haenamichnus uhangriensis* from Korea, representing the largest known pterosaur tracks. In the latest Cretaceous (Maastrichtian), there are multiple records of neozhdarchian tracks in North Africa and North America, with occurrences extending close to the Cretaceous-Paleogene boundary.⁹⁷

Testing paleoecological and evolutionary hypotheses using tracks

The track record represents an underutilized yet invaluable resource for testing functional, paleoecological and evolutionary hypotheses in ways that body fossils alone cannot achieve. Both body fossil and track records are subject to distinct environmental and sampling biases that limit interpretations of pterosaur ecology and evolution.^{4,29,36,98} Due to their different preservation processes, these records provide semi-independent accounts of pterosaur history. Comparing these records, while acknowledging their individual limitations, enables a more nuanced understanding of pterosaur biology, behavior, and evolution.

For instance, it has been proposed that changes in pterosaur body plans during their evolutionary history reflect shifts in their non-aerial locomotor ecologies. Specifically, non-pterodactyloid pterosaurs are thought to have been primarily adapted for arboreal or scansorial lifestyles, whereas the emergence and diversification of pterodactyloids coincided with a transition toward autopodia adapted for terrestrial locomotion.^{2,19,36}

Variation in autopodial proportions further supports this ecological shift. Although non-pterodactyloids display traits indicative of scansoriality, the autopodia of pterodactyloids show increasing adaptation to terrestrial locomotion during their later evolutionary history. This transition is most pronounced in four major clades: Ctenochasmatoidea, Pteranodontia, Dsungaripteridae, and Neozhdarchia.¹⁹

The ability to identify pterosaur trackmakers provides an independent line of evidence to test hypotheses about pterosaur locomotor ecology based on skeletal anatomy. This approach predicts that tracks made by scansorially adapted non-pterodactyloids would be rare or absent in the fossil record, whereas pterodactyloid tracks would be more abundant. In addition, tracks from those pterodactyloids without terrestrially adapted

autopodia (istiodactylids, ornithocheirids, and tapejarids) should be rare or absent, whereas tracks from pterodactyloids with terrestrially adapted autopodia (ctenochasmatooids, pteranodontians, dsungaripterids, and neozhdarchians) would form most of the track record (Figure 7).

These predictions align closely with observed patterns in the pterosaur track record. Tracks are entirely absent from the early part of pterosaur evolutionary history, including the Upper Triassic and Lower Jurassic, when only non-pterodactyloids were present (Figure 7). Indeed, tracks attributable to non-pterodactyloids have yet to be found.⁹⁹

Recognizing the retention of a relatively elongate pedal digit V in some ctenochasmatooid pes prints alleviates concerns about the potential for non-pterodactyloid tracks to be incorrectly assigned to pterodactyloids.^{14,25} A synapomorphy-based approach provides a robust framework for distinguishing pterodactyloid tracks from those of non-pterodactyloids, regardless of whether pedal digit V in non-pterodactyloids contacted the substrate during locomotion.¹⁴ By focusing on derived traits, such as the distinctive metatarsal proportions of ctenochasmatooids (Figure 7A), we can confidently rule out misclassification of non-pterodactyloid tracks.

The question of whether non-pterodactyloids were competent terrestrial locomotors remains unresolved, perhaps in part because no clear consensus exists on what constitutes “competent” terrestrial mobility. The absence of any trackway evidence significantly impedes our understanding of non-pterodactyloid terrestrial locomotor capabilities. Given that the basic stance and terrestrial locomotor modes of pterodactyloids were only accepted after the discovery of their trackways—and even then, after considerable debate—it seems unlikely that the terrestrial locomotor capabilities of non-pterodactyloids can be resolved without trackway evidence. Therefore, we refrain from making definitive claims about their potential terrestrial capabilities. Although the absence of non-pterodactyloid trackways does not necessarily suggest terrestrial incompetence,¹⁴ it is consistent with the hypothesis that terrestrial locomotion was neither their primary nor habitual non-aerial locomotor mode. This aligns with anatomical evidence indicating that non-pterodactyloids were adapted to scansorial or arboreal lifestyles.¹⁹

Similarly, tracks are not known for pterodactyloid groups such as istiodactylids, ornithocheirids (“ornithocheiromorphs”), and tapejarids, which appear least well adapted for terrestrial locomotion. These groups lack the elongated proximal phalanges and reduced distal phalanges that are characteristic of terrestrially adapted tetrapods—a trait observed in all known pterosaur track morphotypes (Figure 7A). This absence is particularly striking given that, collectively, these groups account for most of the known pterosaur diversity during the Lower Cretaceous.⁷⁸ However, it is generally agreed that “ornithocheiromorphs” were unlikely to have engaged in frequent or prolonged terrestrial locomotion due to their greatly reduced pelvic, hindlimb, and autopodial skeletons.^{2,3}

The paleoecology of tapejarids remains unresolved, with conflicting views on their non-aerial locomotor habits. Some propose a predominantly terrestrial lifestyle based on skeletal similarities to other azhdarchoids,^{3,100} whereas others argue for arboreality, citing distinct autopodial anatomy.^{19,72,101} The

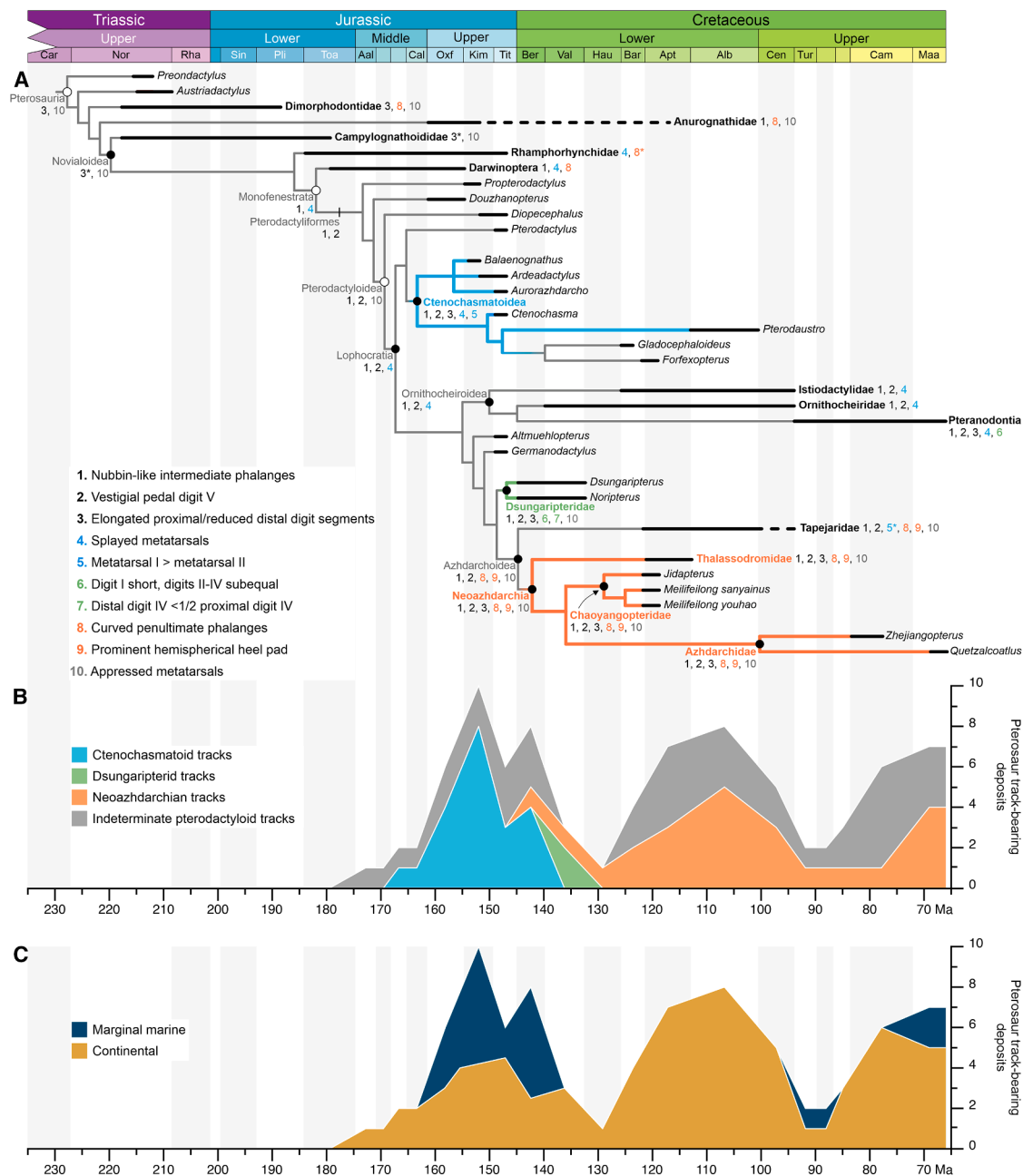


Figure 7. Phylogenetic distribution, trackmaker abundance, and environmental occurrence through time

(A) Simplified pterosaur phylogeny⁶⁹ pruned to include pterosaur taxa with known pedal morphology, alongside a character map of traits present in elite pterosaur pes prints. Characters 1–3 are shared by all prints, characters 4–5 define morphotype 1, characters 6–7 occur in morphotype 2, and characters 8–9 are found in morphotype 3. Character 10 is shared by morphotypes 2 and 3. An asterisk (*) indicates the occurrence of a character in some members of a clade. Node-based clades are indicated with black circles, apomorphy-based clades with white circles, and branch-based clades with a through line.

(B) Abundance of tracks attributed to each of the three track-making clades, as well as indeterminate pterodactyls.

(C) Occurrence of pterosaur tracks in both marginal marine and continental deposits over their evolutionary history. Refer to Figure S6 for the distribution of marginal marine and continental occurrences for each of the three track morphotypes.

See Data S1 for more details.

absence of tapejarid tracks in the fossil record suggests ecological differences from neoazhdarchians. This may reflect differences in locomotor ecology, as arboreal tapejarids would rarely produce tracks. Alternatively, feeding ecology could explain their

absence; if tapejarids were frugivorous or herbivorous,²¹ they may have avoided the vegetation-poor environments, such as mudflats and sandflats, where pterosaur tracks are typically preserved.

Pterodactyloid track morphotypes 1, 2, and 3 correspond to three of the four most terrestrially adapted pterodactyloid clades, with the track record largely reflecting their temporal distribution (Figures 6, 7A, and 7B), with only pteranodontians absent from the track record, possibly explained by their ecological characteristics. Ctenochasmatooids, dsungaripterids, and neoazhdarchians are all considered to have been heavily dependent upon terrestrial or marginal aquatic environments.^{3,15,16} By contrast, pteranodontians are widely considered to have been oceanic wanderers, and are the only major pterodactyloid group to be exclusively recovered from marine deposits.^{102,103} Why the autopodia of pteranodontians differ so fundamentally from those of other ornithocheiroids remains to be determined, but adaptation to aquatic propulsion/take-off appears the most probable explanation.³

Ctenochasmatooid tracks are predominantly found in marginal marine tidal flats (Figures 7C and S6A), often in high abundance, forming a significant component of vertebrate ichnoassemblages, such as those in the Sundance Formation (western USA)³⁷ and La Plage aux Ptérosaures in the Cazals Formation (southwest France).¹⁰ Such abundance demonstrates that ctenochasmatooids were not just present within these specific environments but were integral, defining aspects of the ecosystems. This distribution aligns with the traditional view of some ctenochasmatooids as filter-feeding waders.^{2,3}

Similarly, the prevalence of dsungaripterid tracks in the Tugulu Group demonstrate that they were a significant component of this deltaic-lacustrine paleoenvironment (Figures 7C and S6B). It is most probable that dsungaripterids were specialist shellfish feeders, characterized by recurved, edentulous jaw tips used to pry prey from the substrate, and a durophagous dentition capable of crushing tough-shelled organisms.^{2,3} Given that evidence of this feeding ecology is highly conducive to fossilization, it is surprising that no pterosaur feeding traces have been reported alongside dsungaripterid footprints. Even more striking is the apparent spatiotemporal restriction of dsungaripterid tracks, despite possessing a feeding ecology seemingly well-suited for preservation in the ichnological record.

The neoazhdarchian track record suggests a somewhat different ecology. Their tracks are found exclusively in continental deposits until the very end of the Cretaceous, when they begin to appear in marginal marine settings (Figures 7C and S6C). Although ctenochasmatooid and dsungaripterid tracks are often the most abundant component of the track surfaces on which they occur, neoazhdarchians are different in that, with the possible exception of the tidal flat Tagragra Formation of the terminal Cretaceous of Morocco,⁷¹ they typically occur as a minor component of more diverse ichnofaunal assemblages.^{97,104,105} This indicates that neoazhdarchians were not as specialized in exploiting marginal aquatic ecosystems to the extent seen in ctenochasmatooids and dsungaripterids. Neoazhdarchian trackways frequently align with the bimodal orientation patterns of terrestrial dinosaur trackways found on the same surfaces, where tracks primarily follow two opposing preferred directions.^{105,106} This suggests that, like dinosaurs, neoazhdarchians typically reacted to water bodies as physical barriers to terrestrial locomotion rather than as areas actively sought for purposes such as foraging.

Consequently, certain proposed neoazhdarchian feeding ecologies, such as probe-feeding, subaquatic tactile feeding,

or heron-like strike fishing, are unlikely to have been representative of the group²¹ as these behaviors would have produced similar ichnological signatures to those of other water-margin specialists, both pterosaurian and avian. Together, these are consistent with the proposal that neoazhdarchians were predominantly terrestrial foragers.^{15,16}

Conclusions

This study demonstrates that detailed analysis of pterosaur pedal anatomy and track morphology, based on quantitative and synapomorphy-based methodologies, enables reliable assignment of pterosaur tracks to trackmakers. Critically, we show that trackmaker identification can, in many cases, be extended beyond “pterosaur” and “pterodactyloid” to more exclusive clades: ctenochasmatooids, dsungaripterids, and neoazhdarchians. This increased precision permits closer integration of body fossil and ichnological records, providing an independent line of evidence for testing hypotheses founded on skeletal anatomy.

The temporal, spatial, and taxonomic composition of the pterosaur ichnological record supports the hypothesis of a mid-Mesozoic invasion of terrestrial ecosystems by pterodactyloids. Tracks of scansorial non-pterodactyloids are entirely absent during the early interval of pterosaur evolution (Late Triassic–Early Jurassic). From the Middle Jurassic onward, pterodactyloid tracks appear and rapidly achieve global distribution. These tracks align with clades hypothesized, based on skeletal evidence, to be the most terrestrially adapted of all pterodactyloids, reinforcing functional-morphological interpretations of their locomotor ecologies.

The ichnological record offers a complementary perspective on pterosaur paleoecology. Track abundance, geological contexts, and preserved behaviors corroborate and enrich interpretations derived from body fossils, underscoring the value of integrating these records for a more comprehensive understanding of pterosaur evolution and paleobiology.

RESOURCE AVAILABILITY

Lead contact

Requests for further resources should be directed to, and will be fulfilled by, the lead contact, Robert Smyth (rs1@leicester.ac.uk).

Materials availability

This study does not report new fossil materials. See [key resources table](#) and Figshare (<https://doi.org/10.6084/m9.figshare.c.7739465>) for materials used in this study.

Data and code availability

- Photogrammetric data for the multivariate analysis of pterosaur tracks are available on Figshare. Figshare data: <https://doi.org/10.6084/m9.figshare.c.7739465>. Original datasets necessary to replicate the results of this study are included in [Data S1](#).
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

ACKNOWLEDGMENTS

We are grateful to Jean-Michel Mazin and Joane Pouech (La Plage aux Ptérosaures, Crayssac, France); Jacob Van Veldhuizen (University of Colorado Museum of Natural History, Boulder, USA); Laura Vietti (University of Wyoming

Geological Museum, Laramie, USA); and J.P. Cavigelli and Melissa Connely (Tate Geological Museum at Casper College, Casper, Wyoming, USA) for facilitating access to specimens in their collections. We also gratefully acknowledge the Bureau of Land Management and the Bureau of Reclamation for their role in managing the public lands from which many of the US track specimens were collected. We sincerely thank the reviewers, Roy Smith and Jens Lallensack, along with two anonymous reviewers, for their valuable feedback. We are also grateful to the editor, Florian Maderspacher, for his support and guidance during the publication process. R.S.H.S. was supported by a NERC studentship awarded through the Central England NERC Training Alliance (CENTA; grant reference NE/S007350/1). P.L.F. was funded by UKRI Frontier Research Grant TRACKEVOL (selected by the ERC). D.M.U. acknowledges financial support from the University of Leicester and the John Templeton Foundation (grant ID 61408).

AUTHOR CONTRIBUTIONS

Conceptualization, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.; methodology, R.S.H.S. and B.H.B.; investigation, R.S.H.S., R.J.B., and D.M.U.; formal analysis and data curation, R.S.H.S., P.L.F., and D.M.U.; visualization, R.S.H.S.; supervision, B.H.B., R.J.B., P.L.F., and D.M.U.; writing – original draft, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.; writing – review and editing, R.S.H.S. and D.M.U.; funding acquisition, R.S.H.S., B.H.B., R.J.B., P.L.F., and D.M.U.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2025.04.017>.

Received: February 17, 2025

Revised: March 27, 2025

Accepted: April 8, 2025

Published: May 1, 2025

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
Agisoft Metashape version 2.1.3	Agisoft	https://www.agisoft.com/downloads/installer/
Meshlab version 2022.2	Meshlab	https://www.meshlab.net/
ParaView version 5.11	Paraview	https://www.paraview.org/
Past v4.17	Hammer et al. ¹⁰⁶	https://www.nhm.uio.no/english/research/resources/past/

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Pterosaur track specimens documented for this study are housed in the following institutions: La Plage aux Ptérosaures, Crayssac (CR); the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP); the Tate Geological Museum, Casper College (TATE); the University of Colorado Museum of Natural History (UCM); and the University of Wyoming Geological Museum (UW). The assignment of other pterosaur tracks was based on the published literature. Metric data for pterosaur autopodia were taken from Smyth et al.¹⁹ See [data collection](#) section below and [Data S1](#) for more information.

METHOD DETAILS

Data collection

Tracks which preserved taxonomically informative information were photogrammetrically documented using the standard protocol for ichnological data.^{47,107} Photographs were taken using a Canon EOS 2000D, except at Crayssac, where a Nikon D850 was used. Photogrammetric data for *Pteraichnus wuerhoensis* was acquired from Li et al.⁴⁰ Photographs were processed into textured meshes using Agisoft Metashape version 2.1.3. The 3D models were scaled and fitted to the horizontal plane using Meshlab version 2022.2. Height maps were generated using ParaView version 5.11. All data used in this analysis are deposited in Figshare (<https://doi.org/10.6084/m9.figshare.c.7739465>).

Landmarks were placed at the midpoints of each footpad. Metatarsal lengths were calculated by measuring the straight-line distance from the metatarsophalangeal joint to the posterior margin of the heel pad, following the long axis of the metatarsal impression. Digit segment lengths were measured as the straight-line distance between successive footpads.

Lengths between the distal interphalangeal joint pads and the tips of the claw impressions were excluded from our analysis for two main reasons. First, in all examined prints, claw impressions exhibited extramorphological distortion, such as drag marks. Second, keratinous claw sheaths are rarely preserved in pterosaur body fossils; in most cases, only the bony ungual is present, rendering true claw length unknown for the majority of taxa. As a result, including claw impressions would introduce significant uncertainty into the analysis.

Skeletal data for pterodactyloid feet were sourced from Smyth et al.¹⁹ Comparison with the skeletal record was restricted to pterodactyloid pterosaurs. As yet, no compelling evidence for non-pterodactyloid trackmakers has been reported. Previous reports of non-pterodactyloid, or “rhamphorhynchoid”, tracks can be categorised into two groups. The first involves *Pteraichnus* tracks, in which a small impression of digit V has been interpreted as possible evidence for non-pterodactyloid affinities.²⁵ However, the presence of a small pedal digit V alone is insufficient to make such an attribution, as all pterodactyloids retain metatarsal V, and most possess a small digit V. Moreover, all examples of *Pteraichnus* tracks that preserve a digit V impression can be shown to have been produced by morphotype 1, ctenochasmatooid pterodactyloids. The second category of purported non-pterodactyloid tracks consists of those that have been incorrectly attributed to pterosaurs but instead represent a different group of trackmakers.^{99,108}

Rationale for using pes prints and not manus prints

Pterosaur manus tracks are far more common than pes prints, and in some tracksites, they are the only preserved pterosaur tracks, possibly due to differences in loading of the manus and pes.¹⁰⁹ However, this analysis focuses primarily on the morphology of pterosaur pes prints rather than manus prints. While manus print morphology may offer some ichnotaxonomic value,²⁶ it is unlikely to resolve issues of trackmaker identity for several reasons.

Firstly, the manus provides less anatomical information at its substrate contact points compared to the pes. Pedal impressions can capture the outlines of up to five metatarsals and five digits from a plantigrade foot, while manus impressions typically only record

three digits from a digitigrade hand. In this regard, pterosaur manus impressions are similar to the digitigrade tridactyl pes prints of many dinosaurs, which can be notoriously challenging to attribute to specific trackmakers with certainty.

Moreover, certain characteristics of pterosaur manus impressions further diminish their effectiveness for identifying trackmakers, even when compared to other tridactyl prints. Unlike other prints where the digits generally align with the direction of travel, the pterosaur manus is strongly rotated laterally. As a result, digit I is typically oriented anterolaterally or laterally, digit II laterally or posterolaterally, and digit III posteriorly. This perpendicular or opposing orientation of the manual digits leads to complex interactions between kinematics and the substrate, resulting in variations in impression depth and width, as well as scouring and shifting, especially during the lift-off phase when digits are dragged through the print. Such scouring obscures much of the anatomical information originally impressed, limiting the amount of anatomical detail preserved in the tracks. Even the coarsest measurements, such as total digit impression length, must be considered provisional with regard to trackmaker anatomy, as the position and extent of the metacarpophalangeal pad(s) cannot be accurately determined.

Spatiotemporal distribution of pterosaur tracks

A comprehensive database of pterosaur tracks from across the globe was developed through an extensive review of published literature, due to the notable absence of ichnological data in existing palaeontological databases. Each entry in the dataset represents individual track morphologies documented from a single stratigraphic unit. Pterosaur track-bearing units were selected as the operational framework for recording these tracks, rather than individual tracksites, to account for biases in collection and geological exposure. Such biases often result in certain units being disproportionately sampled across numerous localities (e.g., Sundance Formation and Huérteles Formations), while many others are represented by only a single tracksite.

The ages of pterosaur track-bearing units were derived from the track literature, along with the first and last reported occurrences of skeletal remains belonging to Ctenochasmatoidea,^{33,66} Dsungaripteridae,^{80,84} and Neoazhdarchia.^{77,83,93} In some instances, the ages of stratigraphic units have been refined since their initial reporting, and these updates are reflected in our dataset. While individual tracksites typically represent brief periods of deposition, the extent of each bar in the stratigraphic diagram indicates the uncertainty in the temporal and spatial distribution of the tracks, rather than the precise stratigraphic range of track deposition.

Misidentified and questionable pterosaur tracks

Reliable identification of pterosaur tracks remains a significant challenge, as distinguishing them from tracks of other organisms may not always be straightforward. Many questionable tracks have been misattributed to pterosaurs or tentatively referred to them without compelling evidence, lacking any diagnostic features. This ambiguity complicates the classification process and highlights the need for a thorough re-evaluation of all track records. Jung and Huh²⁶ identified purported pterosaur tracks from 11 distinct stratigraphic units as of questionable validity. Building on their work, we argue that there is insufficient justification to assign tracks from most of these units to pterosaurian trackmakers. This is largely due to misidentification or the absence of diagnostic characteristics that would unequivocally link these tracks to pterosaurs rather than other potential trackmakers. In addition to the track identifications questioned by Jung and Huh,²⁶ we find that purported pterosaur tracks from several other deposits also cannot be reliably attributed to pterosaurs. However, the methodology applied in this study confirms that some previously ambiguous tracks, such as those within the Blackhawk Formation, can now be confidently attributed to pterosaurs. A review of misidentified or questionable pterosaur tracks is provided below.

Jurassic

Turners Fall Formation

Antipus flexiloquus from the Lower Jurassic Turners Fall Formation is generally recognised as a crocodylomorph trace.^{110,111} However, on one occasion it was suggested that it may have been produced by a pterosaur.¹¹² The presence of pentadactyl manus prints in *Antipus flexiloquus*, positioned closer to the trackway midline than the pes prints, is sufficient to rule out any further consideration of a pterosaur trackmaker.¹¹⁰

Clarens Formation

*Saltirecarpines tinleyi*¹⁰⁸ from the Lower Jurassic (Pliensbachian-Toarcian) Clarens Formation¹¹³ has been reported as a potential hopping pterosaurian track. However, it is highly unlikely that pterosaurs, none of which are considered bipedal, could be responsible for this trace. The identification of this track as having been specifically produced by a pterosaur lacks any morphological comparisons to support it. Van Dijk and Eriksson¹⁰⁸ propose alternative archosaurian trackmakers and frequently refer to the trackmaker as dinosaurian, only to suggest, without explanation, at the end of the publication that a pterosaur may have produced the tracks. There is no basis for assuming that these prints were made by a pterosaur. Rather than a hopping biped, these prints likely represent 'swim tracks' of a crocodylomorph.¹¹⁴

Navajo and Aztec Sandstone

We agree with Lockley et al.²⁵ that the poorly defined tracks reported from the Lower-Middle Jurassic Navajo Sandstone and Aztec Sandstone Formations lack the diagnostic morphological characteristics necessary for a reliable referral to Pterosauria. Other potential trackmakers are currently more plausible, and therefore, more compelling material is needed to support any claims of pterosaur tracks in these units.

Saltwick Formation

Traces from the Middle Jurassic (Aalenian) Saltwick Formation that have been referred to *Pteraichnus*¹¹⁵ cannot be reliably verified. The presence of potential manus prints, which may or may not be tridactyl, along with a tridactyl pes, does not provide sufficient justification for assignment to *Pteraichnus* or a pterosaur trackmaker. There is a lack of distinctive features necessary for the confident identification of a specific trackmaking organism.

Other possible tracks from the Saltwick Formation are unlikely to have been produced by pterosaurs. The enigmatic trace *Pseudopteraichnus whitbyensis* was compared with both *Pteraichnus* and the xiphosuran trackway *Kouphichnium*.¹¹⁶ The identity of the trackmaker remains unresolved but reported similarities to pterosaur tracks are unconvincing, sharing only “pes” prints that appear to be tetradactyl and with elongate “heel” impressions. The relative positions of the “pes” prints are inconsistent with known pterosaur trackways. “Digit” lengths and divarication, particularly in “pes” print B are unlike those observed in any known pterosaur body fossil taxon or ichnogenus. The so-called “overprinted manus impression” is inconsistent in shape and position (misfitted contralaterally) and more likely a case of pareidolia within the imprint. Until more compelling evidence emerges, there is no reason to assume pterosaur tracks are present in the Saltwick Formation.

Azóia and Lourinhã Formation

None of the purported pterosaur tracks reported from the Upper Jurassic of Portugal can be substantiated.¹¹⁷ The two tridactyl manus prints from the Azóia Formation are inconsistent with known pterosaur tracks, as all three digits are of nearly equal length and oriented anteriorly in the direction of travel. This is inconsistent with the laterally rotated manual digits of all known pterosaur tracks. Similarly, a supposed manus and partial pes from the Lourinhã Formation lack any diagnostic pterosaurian features, offering no clear distinction from other potential trackmakers.

Cretaceous

San Juan Raya Formation

Prints reported as probable pterosaur tracks from the Valanginian-Hauterivian San Juan Raya Formation are unlikely to represent pterosaurs.¹¹⁸ A figured tetradactyl pes print clearly shows an associated tetradactyl or pentadactyl manus print positioned antero-medially, a configuration inconsistent with pterosaur tracks but typical of crocodylomorphs.

Gething Formation

Two tracks reported from the Lower Cretaceous (Hauterivian–lower Albian) Gething Formation were excluded from consideration as possible *Pteraichnus* manus impressions.¹¹⁹ These tracks more likely represent collapsed impressions of the “four-toed theropod” tracks which occur on the same surface. One of these theropod pes prints (C4) bears a close resemblance to the proposed *Pteraichnus* impressions and can only be distinguished from these supposed pterosaur tracks because it forms part of a recognisable theropod trackway.

Patuxent Formation

None of the purported pterosaur tracks from the Lower Cretaceous (Aptian) Patuxent Formation can be confidently assigned to pterosaurs.^{120,121} Casts of isolated prints are ambiguous showing little more than vaguely tridactyl impressions (e.g., UCM 199.38, UCM 199.39, UCM 199.43), which may represent partially collapsed, widely divaricating pes prints of theropods known from the ichnoassemblage. Other pes prints, such as UCM 199.40, UCM 199.41, UCM 199.42, and UCM 199.61, are clearly attributable to crocodylomorphs.

Several crocodylomorph manus prints, previously interpreted as tridactyl, can only be classified as such because the slabs on which they occur are incomplete, truncating the medial digits (e.g., UCM 199.42, UCM 199.61). Others, such as UCM 199.40, are at least tetradactyl and lack a deeply impressed metacarpophalangeal region, incompatible with pterosaur manus morphology. Additional prints reported from the NASA Goddard Space Flight Center suffer from similar issues and therefore cannot be reliably attributed to pterosaurs.¹²¹

Songdo Formation

A brief reference has been made to the occurrence of pterosaur tracks in the early Campanian Songdo Formation of Soak Island, South Korea.¹²² However, due to insufficient documentation, it is not possible to verify this report.²⁶

Zhutian Formation

A single pes print from the Upper Cretaceous (Maastrichtian) Zhutian Formation is partially obscured by mudcracks, rendering its key features ambiguous.¹²³ While it is interpreted as tetradactyl, the number of digits cannot be determined from the available image. Although the print has been attributed to a pterosaur, we find the evidence insufficient to confirm the presence of pterosaurs in the assemblage.

Blackhawk Formation

The status of pterosaur tracks from the Upper Cretaceous (Campanian) Blackhawk Formation is more complicated. Manus-only tracks from a mine west of Helper near Price are probably referable to pterosaurs,^{8,124} though the absence of direct access to the material precludes definitive verification.

In contrast, there is no valid basis for assuming that any of the purported pterosaur tracks from Meetinghouse Canyon were produced by pterosaurs.¹²⁵ The parallel scratch marks observed cannot be justifiably assigned to a pterosaurian trackmaker. Additionally, a manus-pes set from Meetinghouse Canyon (UCM 225.13) is demonstrably non-pterosaurian. The manus impression is heavily kinematically altered, but exhibits at least a tetradactyl, if not pentadactyl, morphology. The pes imprint features broad, fleshy soft-tissue pads, resembling those of crocodylomorphs rather than the discrete, small digital pads typical of pterosaurs. Furthermore, the

manus print is situated closer to the track midline than the corresponding pes impression, a configuration inconsistent with pterosaur track patterns. Lastly, a prominent, sinuous tail drag mark along the likely trackway midline conclusively demonstrates that the track-maker was a crocodylomorph.

Swim track dominated ichnoassemblages

We have excluded from our assessment of the pterosaur record several Cretaceous units containing only parallel tridactyl and/or tetradactyl scratch marks, interpreted as swim tracks, that lack identifiable manus and pes prints. This includes all purported tracks from the 'mid' Cretaceous (Albian-Cenomanian) Dakota Group, Dunvegan Formation,^{8,126} Kem Kem Group¹²⁷ and the Upper Cretaceous (Maastrichtian) Escondido Formation.¹²⁸

It has been proposed that the relative proportions of these scratch marks support their attribution to pterosaurs, as many (though not all) exhibit two central scratches longer than the outer ones. This pattern is consistent with the pedal morphology of many pterosaurs, where digits II and III are longer than digits I and IV. However, this feature alone is insufficient to conclusively assign these tracks to pterosaur trackmakers. Even minor variations in pes movement or the degree of substrate contact can produce different scratch mark patterns or affect the number of digits recorded in a swimming trace. Given the absence of verifiable pterosaur tracks in these units and the presence of more plausible trackmakers, such as crocodylomorphs or turtles, attributing these traces to pterosaurs currently appears to be an overly speculative and unparsimonious interpretation.

Phylogeny and character mapping

A simplified version of a pterosaur phylogeny was reproduced,⁶⁹ focusing on pterosaur taxa with known pedal morphology. The tree was pruned to include only those taxa with sufficient data on pedal traits. A character map was then created, highlighting traits observed in 'elite' pterosaur footprints. Characters 1–3 are shared by all prints. Characters 4–5 corresponded to traits observed in European and South American ctenochasmoids, with character 5 being absent in Chinese ctenochasmoids. Characters 6–7 co-occur in dsungaripterids, while characters 8–9 are observed in neoazhdarchians. Character 10 is present in both dsungaripterids and neoazhdarchians. The occurrence of specific characters in some clade members was noted using an asterisk (*) to indicate variability within certain lineages.

To be identified as potential trackmakers, pterosaur body fossil taxa had to preserve all of the necessary traits: 1, 2, 3, 4, and 5 for ctenochasmoids; 1, 2, 3, 6, 7, and 10 for dsungaripterids; and 1, 2, 3, 8, 9, and 10 for neoazhdarchians. However, the presence of character 9 (prominent heel pad) had to be inferred for neoazhdarchians based on the ancestral state of Azhdarchoidea, due to the absence of preserved pedal soft tissue in the group.

QUANTIFICATION AND STATISTICAL ANALYSIS

Morphometric data and analyses

The pterodactyloid pes multivariate dataset includes 62 specimens, representing 22 taxa with near-complete pedal skeletons. The pterosaur track dataset includes 32 pterosaur pes prints from 15 localities in 8 stratigraphic units.

The quantitative analyses presented here require reliable identification of soft tissue landmarks that delineate the boundaries of underlying skeletal proportions. Consequently, every pes print included in our study needed to preserve all 12 corresponding soft tissue structures, which must be clearly defined. These structures include the heel print, metatarsophalangeal joints I–IV, proximal interphalangeal joints of digits II–IV, and distal interphalangeal joints of digits I–IV. Prints also had to show no signs of significant post-formational modification; however, the stringent soft tissue criteria typically mitigated this concern.

Landmarks were placed at the midpoints of each footpad. Metatarsal lengths were calculated by measuring the straight-line distance from the metatarsophalangeal joint to the posterior margin of the heel pad, following the long axis of the metatarsal impression. Digit segment lengths were measured as the straight-line distance between successive footpads.

Lengths between the distal interphalangeal joint pads and the tips of the claw impressions were excluded from our analysis for two main reasons. First, in all examined prints, claw impressions exhibited extramorphological distortion, such as drag marks. Second, keratinous claw sheaths are rarely preserved in pterosaur body fossils; in most cases, only the bony ungual is present, rendering true claw length unknown for the majority of taxa. As a result, including claw impressions would introduce significant uncertainty into the analysis.

Skeletal data for the pterosaur foot were adapted from Smyth et al.¹⁹ to align the positions of joints with the corresponding footpads. As most pterosaur footpads are arthral, the lengths of most elements corresponded to the distances between joints, and thus no modifications were necessary. Consequently, the lengths of the metatarsals, as well as digits I, proximal digit II, and distal digit II, were directly based on the lengths of their respective skeletal elements (MT I–IV, PPh I-1, PPh II-1, and PPh II-2). However, due to the anatomical arrangement in pterodactyloids, where the proximal interphalangeal joints of digits III and IV enclose PPh III-2 and PPh IV-2/IV-3, respectively, modifications were made to better represent these features. Specifically, the length of proximal digit III was set to equal PPh III-1 plus half the length of PPh III-2, while the length of distal digit III was defined as half the length of PPh III-2 plus PPh III-3. For digit IV, proximal digit IV was calculated as the sum of PPh IV-1 and PPh IV-2, and distal digit IV was set as the sum of PPh IV-3 and PPh IV-4.

Analyses of pterosaur skeletal and track data were performed using PAST version 4.13.¹⁰⁶ To mitigate the impact of absolute body size on the results, data were normalized following a modified version of the protocol of Smyth et al.¹⁹ Each segment was divided by the total length of pedal ray III excluding ungual or claw impression.

In multivariate analyses, skeletal specimens were grouped according to those of Smyth et al.¹⁹ Ichological data was grouped by the geological formation/locality as most pterosaur track assemblage appears to be monotypic, representing either a single track-making taxon or several closely related taxa with similar hand and foot morphologies.

Comparison with the skeletal record was restricted to pterodactyloid pterosaurs. As yet, no compelling evidence for non-pterodactyloid trackmakers has been reported. Previous reports of non-pterodactyloid, or 'rhamphorhynchoid,' tracks fall into two categories. The first involves *Pteraichnus* tracks, in which a small digit V impression has been interpreted as supporting non-pterodactyloid affinities.^{25,129} However, a small pedal digit V impression alone is insufficient for such an assignment, as all pterodactyloids retain metatarsal V, and most possess a small digit V. As discussed, these tracks exhibit clear synapomorphies with ctenochasma-toids, so non-pterodactyloid trackmakers can be excluded.

Peters¹³⁰ assigned numerous tracks to both non-pterodactyloid and pterodactyloid trackmakers. However, reliance on idiosyncratic digital reconstruction methods, which diverge from well-established anatomical and ichnological morphology,^{131–133} undermine the conclusions of this work. Like previous studies, our direct examination of the material could not identify many of the proposed features in pterosaur skeletal anatomy and track morphology, casting significant doubt on the validity of these trackmaker assignments.

The second category of purported non-pterodactyloid tracks including *Rhamphichnus* spp., are not pterosaurian.³⁸ Examination of the *Rhamphichnus* material reveals a trackmaker with a pentadactyl manus and tetradactyl pes, with manus impressions closer to the trackway midline than the pes prints, excluding a pterosaurian interpretation (Figure S7). These tracks likely represent crocodylomorph trackmakers,⁹⁹ with differences between the three ichnospecies reflecting variations in trackmaker gait and substrate properties, rather than distinct trackmaking organisms. Additionally, *Rhamphichnus* occurs on surfaces that preserve other crocodylomorph tracks, many of similar size, and sharing similar trackway orientations.³⁸ Another example is *Saltirecarpipes tinleyi*,¹⁰⁸ which shares with non-pterodactyloids only one possible feature, a functionally tetradactyl, ectaxonic pes. This trait is also found in crocodylomorphs.¹¹⁴